Ecology of ecosystems and biotic communities

van de Koppel, Johan; van Andel, Jelte; Biere, Arjen

Published in:
Restoration Ecology

Publication date:
2012

Chapter 6

ECOLOGY OF ECOSYSTEMS AND BIOTIC COMMUNITIES

Johan van de Koppel, Jelte van Andel and *Arjen Biere*

Restoration Ecology: The New Frontier, Second Edition. Edited by Jelte van Andel, James Aronson.

6.1 INTRODUCTION

The focus of restoration ecology, and the closely allied practice of ecological restoration, is the structure, composition and functioning of ecosystems in a given landscape. Recall that an **ecosystem** encompasses the interactions between species of a **biotic community**, and between each of them and the abiotic environment in which they live. Recall also that a **landscape** is made of an assemblage of interacting systems, including ecosystems, each with its own community. In the present chapter, we start by giving a brief history of successive scientists' views on the subject of ecosystems as an ecological unit. Thereafter we present a number of examples of direct and indirect interactions between and among species within a biotic community, which in turn affect community structure and, at a higher level still, whole-ecosystem functioning. Then, we consider complexity in species interactions as a variable to be considered for those studying or attempting to carry out ecosystem restoration in a world of environmental change. At the end of each section, we indicate the impact that our exposé may or should have on the further development of the science of **restoration ecology**. We conclude by reflecting on the desired 'attributes of restored ecosystems' as given by *SER Primer on Ecological Restoration* (SER 2004), and on the interface between theory and practice in general.

6.2 ECOSYSTEMS

The views that ecologists have of ecosystems have developed and evolved enormously since the term was first introduced, 75 years ago, by A.G. Tansley (1935). Among other things, it changed as a result of the way that successive generations of ecologists, anthropologists, and archaeologists considered so-called 'natural' systems. Until recently, a 'balance of nature' paradigm prevailed, so let's begin our survey there.

6.2.1 Ecosystems in a supposedly 'balanced' world

The field of ecosystem ecology traditionally studies fluxes of energy and matter through and between ecosystems. The first studies on the functioning of ecosystems focused on the transfer of energy, and how energy fluxes determine productivity of plants, and the herbivores and predators that perch higher in the food chain. A seminal paper was that of Lindeman (1942), who studied fluxes of energy (derived from the biomass of different feeding or trophic levels) through the aquatic food web of Cedar Bog Lake in Minnesota. His example was followed by a whole generation of ecosystem ecologists, inspired by Eugene P. Odum, among others (see Golley 1996). Their work highlighted the structuring effects of energy flow in ecosystems, limiting productivity of successive *trophic levels* as progressively less energy is available when moving from primary producers (e.g. plants and algae) via herbivores to predators and, finally, the top predators. As every trophic level beyond the first one respires and discards (as urine and faeces) part of its consumption, less energy is available for higher trophic levels. As a consequence, food chains and food webs often have a pyramidal shape when biomass or energy is expressed per trophic level.

Ecosystem ecologists soon found that ecosystem productivity is determined not only by fluxes of energy, but also by nutrient flows (see e.g. DeAngelis 1992). All organisms require and take up a certain proportion of macronutrients (e.g. nitrogen and phosphorus, or silicate, in the case of diatoms), as well as numerous minor or oligo-elements. These nutrients are necessary for organisms to build new tissue and to compensate for tissue turnover. In many ecosystems, energy and carbon (a major element of carbohydrates) are not the limiting factor to the growth of organisms; rather, it is the limited availability of nutrients for part or all of the year. A key difference here is that availability of nutrients is not so much determined by input and output from the ecosystem but rather depends much more on local sources such as mineralization of nitrogen through the decomposition of dead plant material. As a consequence, the pathways followed by these nutrients moving through the ecosystem often appear to be cyclic, rather than linear, as is generally the case for energy and carbon.

At the heart of the aforementioned approaches to ecosystem ecology lies the notion that most natural ecosystems, most of the time, are 'in balance', thanks to **resistance** and **resilience** that develop as emerging attributes of ecological systems over evolutionary time. In other words, except when an ecosystem is heavily disturbed by humans or by catastrophic disruptions such as earthquakes or volcanic eruptions, the system stays in some sort of equilibrium. This implies that the inputs and outputs of an ecosystem, including

births and deaths, and migrations and colonizations, roughly match.

Though knowledge of *feedback* relations is crucial to understanding the dynamics of ecosystems and their response to changed conditions, this notion was soon questioned by people studying real ecosystems, who found that many ecosystems are never in equilibrium (Ellis & Swift 1988). Rather, ecosystems are constantly in flux and adapting to changing conditions at various spatial and temporal scales, including changes in climate and in external inputs of nutrients (see also Chapter 21). To understand ecosystems, it is essential to know how they respond to variations in background conditions.

6.2.2 Ecosystems in a world of change

Environmental changes have always occurred, as testified by records of variation in mean global temperature over several thousand years (Intergovernmental Panel on Climate Change (IPCC) 2007b). However, our very rapidly growing human **ecological footprint**, over the last two centuries especially, is causing profound and sometimes very rapid changes in environmental conditions on our planet – due for example to industrial, agricultural, and urban greenhouse gas emissions and the artificial enrichment of aquatic ecosystems by inorganic nutrients, especially N and P, 'leaking' from intensively fertilized fields and choking out possibilities for life through **eutrophication**. This has led ecologists to ask the question 'How do ecosystems respond to these changes?'

The presence of feedback relations within ecosystems is not always an adequate safeguard against potential effects of rapid and/or profound changes in environmental conditions. In particular, some systems change significantly, even violently, in response to shocks and stress induced by profound or prolonged human influences. A striking example of this is shallow lakes, as reported by Scheffer *et al.* (1993). Many shallow lakes have experienced increased inputs of nitrogen and phosphorus as a consequence of uncontrolled seepage of field and garden fertilizers, and dumping of phosphate-based detergents. Initially, this only leads to minor effects, as long as increased densities of dead and decomposing aquatic plants locked up the nutrients in the sediment, generating a *feedback loop* that compensates, in part, for increased nutrient availability. As nutrient inputs increase further, especially of phosphorus, a shift or transition takes place, as conditions become ideal for microalgae. In the presence of unusually high nutrient levels in the water, therefore, many shallow lakes rather suddenly switch from a state with clear water and a highly diverse community of aquatic plants and invertebrates, to a murky water state, with a much less diverse community of pelagic microalgae. Submerged aquatic plants disappear, and in some cases, large populations of toxic cyanobacteria proliferate. The faunistic community in this new state is characterized by sediment-feeding fish, which exploit and remobilize the phosphorus that is stored in dead plant material in the sediment, generating a feedback loop that solidifies or 'fixes' the microalgae-dominated state in which the lakes now occur (see also Chapter 18).

The change in ecosystem state that these shallow lakes experience in response to increased eutrophication was unexpected, dramatically fast and hard to reverse. Many lakes stay in their murky state for years after anthropogenic nutrient inputs are stopped, and nutrient levels must return to levels well below those at which the initial switch to a microalgae-dominated state occurred before submerged plants are able to recover. At the basis of this lies a phenomenon whose existence was predicted by Noy-Meir (1975), who proposed that not just one but two different 'steady states' may occur in a subtropical or semi-arid region grazing system.

Indeed, we now know that many ecosystems can manifest two or more **alternative stable states**, each characterized by a distinctly different community with different feedback processes and overall functionality. Severe or ongoing human pressure on ecosystems can overwhelm the feedback processes that characterize one state, leading to a dramatic shift from one type of community to another. This new state typically has its own stabilizing feedbacks – in other words, it can become resilient and such that a quick return to the earlier steady state is effectively blocked. Only a dramatic change in conditions will allow a return to the previous state in which the previous biotic community can re-establish itself (see e.g. Suding *et al.* 2004).

Theory on the potential of such 'catastrophic changes' in ecosystems in response to (gradually) changing conditions dominated ecosystem ecology during the late 1990s and early 2000s. The resulting models on alternative stable states, that were obtained primarily from studies of shallow lakes, were subsequently applied to a range of other ecosystems in

attempts to explain dramatic shifts in response to anthropogenic or natural environmental changes. These include semi-arid grasslands (Rietkerk & van de Koppel 1997), coral reefs (Knowlton 1992), wet dune-slacks (Adema *et al.* 2002) and rocky shores (Petraitis & Latham 1999), where large and sudden changes in ecosystem state have been observed. The success of these attempts to apply the aforementioned models of alternative stable states was limited (Bertness *et al.* 2002). Apart from a lack of experimental evidence, an important reason for this is that the theory and models developed for semi-enclosed, relatively homogeneous bodies of shallow-lake water were not sufficient to explain the dynamics of open, spatially extended and heterogeneous ecosystems such as those listed above. In ecosystems such as those, the interplay between local feedback relations between organisms and their respective environments and feedback processes occurring at large scales, generates complex dynamics that can lead them to respond in unexpected ways. Thus, a more complex theory is required to predict how these ecosystems respond to changing environmental conditions. Such a theory should explicitly take into account feedback relations and interactions that cross spatial scales, as discussed in the next section.

6.2.3 Spatial self-organization

When ecologists observe spatial patterns in ecosystems, typically they seek the cause or mechanism in environmental variations at the local or regional levels of organization. Although this is valid in many cases, a number of studies over recent decades revealed clear and consistent spatial variation in the structure of ecosystems in landscapes that exhibit no underlying variation in environmental conditions and can be explained by so-called *spatial self-organization*, a process whereby internal interaction between biotic and abiotic components of an ecosystem generates complex but recognizable and repeated spatial patterns (Rietkerk & van de Koppel 2008; see Figure 6.1). Spatial self-organization has been suggested as the mechanism in nature that leads to the creation of regular patterns, such as those found in the vegetation of some semi-arid land systems (Klausmeier 1999) or peatlands (Rietkerk *et al.* 2004a), as well as the irregular patterns found in mussel beds on wave-disturbed rocky shores (Guichard *et al.* 2003), and in some Mediterranean grasslands (Kefi *et al.* 2007).

We elaborate here on the example of banding or patchy vegetation patterns as found in arid and semi-arid lands in the African Sahel, Australia and elsewhere, which have been much studied (e.g. Valentin & d'Herbes 1999; Tongway *et al.* 2001). In this case, once again, a recurrent research question has been whether or not such patterns result from pre-existing environmental heterogeneity, from spatial self-organization or from both. Klausmeier (1999) analysed a series of spatially explicit models and showed that the patterns can be explained by spatial self-organization alone, that is they are caused by one single mechanism (cf. Thiery *et al.* 1995; Valentin *et al.* 1999). Banded or patchy vegetation promotes the infiltration of water into the soil, a process which benefits vegetation growth under arid or semi-arid conditions. In vegetated bands or patches, more water infiltrates than in bare patches. Overland flow, in particular on hill slopes, then generates a net flux of water into the vegetated patches, and decreases water availability in the bare patches. This interaction between vegetation, water infiltration, and overland flow of water fully explains the formation of spatial patterns involving so-called **runoff** and **run-on** areas, and can thus be considered as spatial self-organization.

Mathematical models indicate that spatial self-organization can have important implications for the functioning of ecosystems (Ludwig *et al.* 1999; Rietkerk *et al.* 2002), in line with indications from empirical work (Valentin & d'Herbes 1999). Indeed, for arid ecosystems, spatial patterns are predicted to compensate for reduced and unpredictable rainfall, allowing for plant growth under conditions that would not sustain plant life if spread homogeneously. This implies that spatial patterns generate *feedback mechanisms* that can compensate for changed environmental conditions, such as drought. Moreover, consistent and predictable changes occur in spatial patterning before the buffering feedbacks are overwhelmed and the system shifts to an alternative state characterized by a bare, degraded landscape (Rietkerk *et al.* 2004b). This provides a basis for the development of indicator systems that can predict sudden shifts between alternative stable states in complex dynamic systems (see below).

6.2.4 Implications for restoration ecology

Insight in the interactions between both negative and positive feedback relations is crucial to understanding

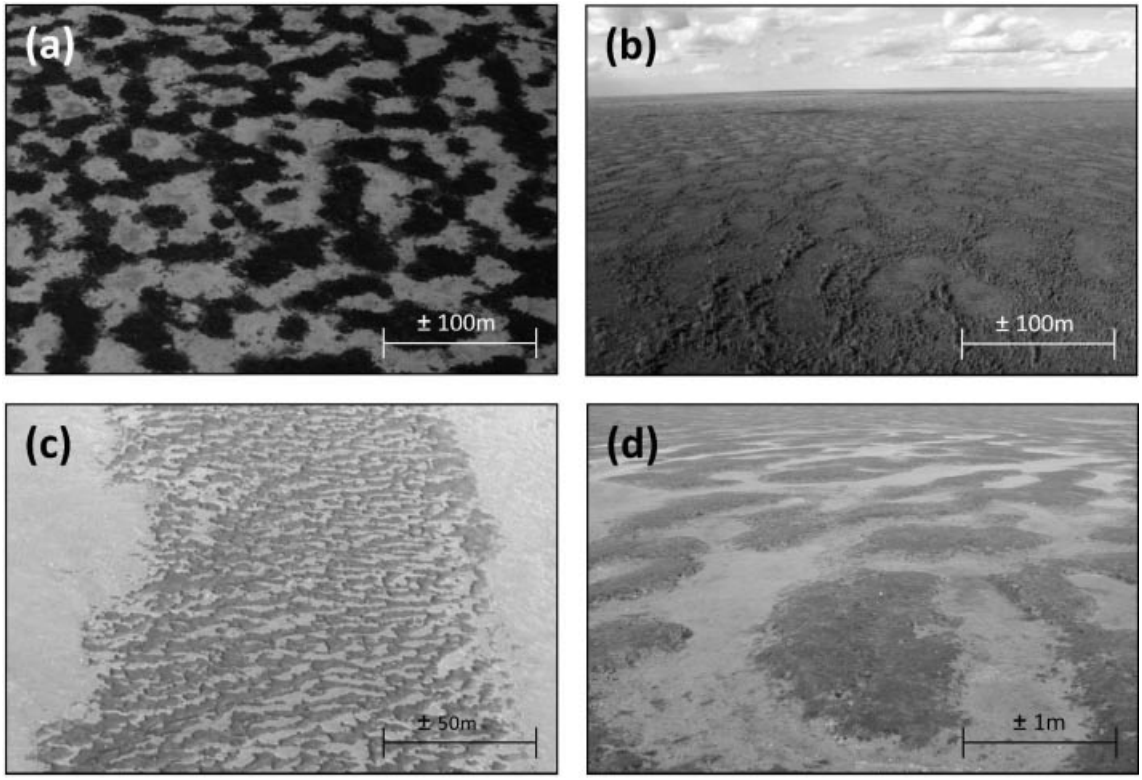

Figure 6.1 Observations of regular patterns from arid ecosystems, boreal wetlands, mussel beds and intertidal mudflats. (a) Labyrinth pattern of bushy vegetation in Niger (scale = 100 m); after Rietkerk *et al.* (2002). (b) Regular maze patterns of shrubs and trees in West Siberia (scale = 100 m); after Rietkerk *et al.* (2004b). (c) Patterned mussel bank in the Wadden Sea, the Netherlands (scale = 50 m); after van de Koppel *et al.* (2005). (d) Labyrinth pattern of marine benthic diatoms in the Netherlands (scale = 1 m); after Rietkerk and van de Koppel (2008). (Photograph (d) by Johan van de Koppel.)

the dynamics of ecosystems and their response to changed conditions. The notion of 'alternative stable states' is particularly relevant to the field of restoration ecology (Suding *et al.* 2004), as their presence is an important determinant of the success of restoration efforts. Indeed, degraded systems may also be resilient. Essential for the conservation and restoration of natural systems is the development of **indicator** systems for so-called *critical transitions* between alternate states, not only in ecological systems such as arid grazing systems (Solé 2007), but also in socio-economic systems such as the financial market (Scheffer *et al.* 2009). Research on this topic is still tentative and in a highly theoretical stage of development, outside the scope of this book, but its applicability may not be far away, for example to identify early-warning signals for future climate change based on understanding of analyses of the past.

When restoring ecosystems to their natural state, it is important to consider that the spatial structure of the original systems was, in part, self-organized, which can have large implications for the functioning and resilience of these ecosystems. Restoration efforts that do not take into account the original spatial structure will likely lead to a community or ecosystem that is more vulnerable to disturbances, supports lower population sizes, and is possibly less species-rich than the pre-disturbance ecosystem. A good example of a restoration project that explicitly took this factor into account was carried out by Tongway and Ludwig

(1996), who performed experiments in a semi-arid region of Australia to rehabilitate degraded landscapes on bare slopes. Their study revealed that the creation of a patchy construction of 0.5 m high piles of acacia branches resulted in a 10-fold increase in water infiltration, with a huge impact on soil quality and plant production (see also Chapter 4). In other words, they improved the recovery potential of the site undergoing restoration by mimicking a natural spatial pattern, and thereby assisting the natural self-re-organization of the ecosystem.

6.3 BIOTIC COMMUNITIES

Biotic communities are not only shaped by the interactions with the abiotic environment, but also to a large extent by all sorts of interactions between different species. Organisms can affect each other by eating, by direct aggressive interference, by changing the environment, and by giving rewards for provisions such as nectar for pollination. In section 6.3.1, we start by describing a number of such direct interactions between species, such as consumption and mutualism. Then, in section 6.3.2, we consider a number of indirect effects that result from these direct physical interactions, such as competition and facilitation. We notice that in many scientific articles, direct interactions are measured by their indirect effects. We consider it essential to explicitly distinguish between the two (i.e. between mechanisms and consequences). While recognizing that the latter are more relevant in ecological restoration projects, how can we manipulate the consequences without knowing the mechanisms? Finally, in section 6.3.3, we reflect on implications of the presented information for restoration ecology.

6.3.1 Direct interactions

As mentioned, we distinguish between direct and indirect interactions between species. We briefly present basic knowledge of the following direct interactions: (1) consumption by plants and animals, with particular attention to interactions between trophic levels, (2) parasitism, a form of consumer–resource interactions, (3) ecosystem engineering of plant and animal species, and (4) mutualisms, especially plant–mycorrhiza and plant–pollinator interactions. This brief overview provides the basis for our understanding of the consequences. Our focus will be on these indirect effects, dealt with thereafter, in view of their impact on ecosystem structure and functioning, which is particularly relevant in the practice of ecological restoration.

Consumption

All organisms require resources to survive, grow and reproduce. At the level of individuals, the benefit is one-sided: a plant needs nutrients and a predator needs prey, but not the other way around. Among animal consumers, there are (monophagous) specialists that consume only one prey species, and (polyphagous) generalists that consume a wide range of prey. Consumption may result in the death of a complete organism, as is the case with many predator–prey interactions, but consumption can also be partial, as for instance when herbivores consume only part of their food plants, or plants absorb small quantities of nutrient pools. Great variations in the relevant temporal scale also occur across the range of interactions where consumption occurs in ecosystems.

The impact of consumption on community structure depends very much on the growth rate or growth potential of the prey species, and the consequences for the food chain or the food web. Imagine a spatial gradient with increasing plant productivity, be it due to increasing annual precipitation in a subtropical region or to increasing nutrient availability in the temperate zones of the Earth (see Figure 6.2). At low productivity, vegetation is too sparse to support herbivores. An increase of primary productivity, however, should

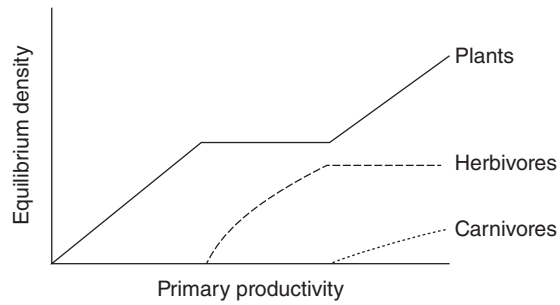

Figure 6.2 The equilibrium densities of plants, herbivores and carnivores as a function of primary productivity. The relationships are based on the model of Oksanen *et al.* (1981). (Modified from van de Koppel 1997.)

attract more herbivores, increasing grazing pressure, maintaining a low standing crop until herbivore biomass is high enough for a population of carnivores to be sustained. From that point in the gradient onwards, the carnivores regulate the herbivore density, and as a result, standing biomass of plants can increase again. This reasoning dates back to the 1980s and is known as the *exploitation ecosystem hypothesis* (EEH), mathematically analysed by Oksanen *et al.* (1981). The model is general and ignores all kinds of variability, such as differences in competitive ability and in resource quality, but it has been a useful starting point for the further development of theories on plant–herbivore interactions. An underlying assumption is, for example, that all vegetation is equally palatable. However, tall plants, and especially the woody parts of them are generally much less attractive to herbivores than herbaceous plants or biomass because stem and wood material is much harder to digest (Fryxell 1991). This holds especially for small grazers, not for browsers. This results in a decrease in the density of grazing herbivores in areas with high plant productivity, even in the absence of carnivores (van de Koppel *et al.* 1996; see Figure 6.3 for an example).

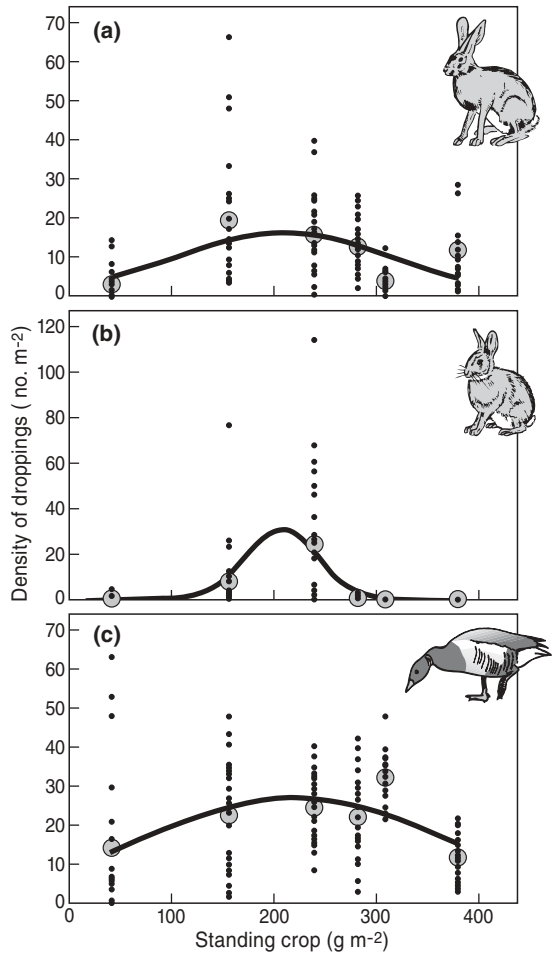

Figure 6.3 Number (means and individual observations) of annual droppings of (a) hares, (b) rabbits and (c) barnacle and brent geese in relation to vegetation standing crop on the coastal salt marsh of the Waddensea Island of Schiermonnikoog, the Netherlands. (Modified from van de Koppel *et al.* 1996.)

Parasitism

Host–parasite interactions are considered as a specific type of consumer–resource interaction, as the parasite consumes tissue of its host, just as in the case of herbivore–plant and predator–prey interactions. Similar models have, therefore, been used for these different types of direct interaction. However, the indirect effects of parasitism on the biotic community may be more dramatic, as illustrated below (section 6.3.2).

Ecosystem engineers

Every living organism changes its environment, by producing shade, by the use and consumption of resources, by excreting various products and so on. Some species create, maintain or modify their environment to such an extent that they significantly affect the growth or survival of other species in their community as well as their own. These plant or animal species, which are often considered as species with a **keystone** or a **foundation** role or position (see Chapter 2), can be called **ecosystem engineers** (*sensu* Jones *et al.* 1994). Note that this term is different from the notion of *ecological engineering*, which is used to indicate human engineering activities (Rosemond & Anderson 2003). Let us now consider two examples of direct interactions: (1) biophysical engineering, such as when beavers make dams, and (2) chemical engineering of the environment, also known as allelopathy in plant communities.

Plant and animal species that physically engineer their respective environments can have long-lasting effects, even beyond their own lifetime (Hastings *et al.* 2007). The North American beaver (*Castor canadensis*),

just mentioned, is a frequently cited example; it creates wetlands and modifies entire landscapes through its damming and foraging activities, which are of course beneficial to themselves but harmful to other organisms. Often, however, the processes are much more subtle and nevertheless influential, such as the burrowing activities and cast constructions of earthworms that alter the mineral and organic composition of soil, accelerate nutrient cycling and facilitate drainage of soils, ultimately affecting the community composition of plants, animals and microorganisms. Direct effects of such biophysical engineering on the part of animals are usually measured by their indirect consequences, such as improving the species' own environment (self-facilitation, as in the case of beavers), or facilitation of other species (as in the case of earthworms). Examples of indirect effects of habitat modification are given in section 6.3.2.

Allelopathy – the release of organic compounds from one plant species, which reduces the germination, growth or fecundity of other plant species in the community – has long been considered as a form of unidirectional interference competition between plants. Here we prefer to consider it as a form of chemical engineering of the environment. There are many thousands of organic plant compounds released from shoot materials or exuded by roots, but only a relatively small number of them have been identified as detrimental and involved in allelopathy. What's more, even if a substance exhibits detrimental effects on plants in laboratory experiments, it might not truly hamper growth of other plant species in the field. A good example of *bona fide* allelopathy is phenolic substances occurring in forest soils (e.g. Hättenschwiler & Vitousek 2000, and references therein). They include, for example, tannins in the leaves of oak trees (*Quercus* spp.) and bracken fern (*Pteridium aquilinum*), where they function as feeding deterrent. Once released from decaying plant materials into the soil environment, phenolics influence plant growth directly by interfering with plant metabolic processes and by their effects on root symbionts. They also affect ecosystem *nutrient cycling* in various ways, and interfere with decomposition, mineralization and humification (see section 6.3.2).

Mutualism

Mutualism is a direct interaction between individuals of different species that results in an increase of fitness for both parties. Mutualistic relationships can be obligate or facultative. Two examples of mutualism that we will illustrate here, as they should be taken into account in restoration projects, are (1) plant–mycorrhiza interactions, and (2) plant–pollinator interactions.

Plant–mycorrhiza interactions can be considered as a mutualistic symbiosis. For the overwhelming majority of vascular plants, mutualistic relationships with mycorrhizal fungi are of utmost importance. Usually, the plant provides the associated fungi with carbohydrates while the mycorrhizae assist their 'host' plants with taking up water and essential nutrients, especially P, Cu and Zn, but also N, K, Mg and Ca (see Kuyper & de Goede 2005 and references therein). However, there are many different types of mycorrhizal fungi (see Ozinga *et al.* 1997 and references therein). Approximately 80% of species of temperate, subtropical and tropical plant communities are infected by *arbuscular mycorrhizal fungi*. These fungi are especially efficient in the uptake of inorganic P and several other relatively immobile ions. *Ectomycorrhizal fungi* occur mainly on woody plants and only occasionally on herbaceous plants and grasses, and they are especially efficient in N-limited ecosystems. *Ericoid mycorrhizal fungi* occur mainly in the Ericales (heathers and heaths) and are physiologically comparable with ectomycorrhizae. Several mycorrhizal fungi have enzymes that break down organic complexes such as tannin and lignin, thereby releasing N and P from organic matter found in the soil, which they then translocate as nutrients in a form that is more readily available to their host plant. This is particularly useful to plants in acid soils, where nutrient uptake by plant roots is often difficult.

Plant–pollinator interactions can be considered as a nonsymbiotic mutualism. The mutualism is opportunistic and flexible rather than fixed, neither symmetrical nor cooperative. The mutual exploitation interest may be skewed towards a consumer–resource relationship between the two parties, or even result in antagonism. In their review on 'endangered mutualisms', Kearns *et al.* (1998) pointed out that over 90% of modern angiosperm species are pollinated by animals of some kind, including insects, birds, lizards, bats and small marsupials. Specialist relationships are much more vulnerable than generalist relationships, but plant–pollinator interactions are only seldom species specific. Indeed, relatively few plant–pollinator interactions are absolutely obligate in a strict sense (Johnson & Steiner 2000). Many flowers show specialization in floral traits, yet they are often visited by diverse assemblages of animals. There is a network of relationships between

the plant community and the pollinator community (e.g. Bosch *et al.* 2009), but the type of network differs from the network of food webs (see section 6.4.1). When pollinators visit flowers of several plant species, this may result in a reduction of seed set for each of the species. Only a few studies on visitation of pollinators include consequences for the fitness of plants in terms of seed set and reproduction (e.g. Kwak & Bekker 2006; Morales & Traveset 2009).

6.3.2 Indirect effects on community structure and succession

In many cases, it is not so much the direct interactions, but rather the indirect effects of resource consumption, parasitism, ecosystem engineering and mutualism that are most influential to community structure and succession, and ecosystem functioning. Here we illustrate a number of such consequences, in the same order as before. Thereafter, we reflect on implications for restoration ecology.

Effects of consumption: competition for resources

Theory of competition is too extensive to be treated in its entirety in this chapter. Readers should consult basic ecology textbooks, such as Krebs (2008), for further ideas and information. Here we focus on competition between plants, as this is the kind of information most relevant for restoration ecologists. Competition for shared resources, and its impact on plant communities, has received much attention from ecologists since the seminal work on the mechanisms of resource competition by Tilman (1982, 1988). Tilman developed a theory based on experiments with micro-algae competing for limiting nutrients until they reached a steady state, and applied it to plants competing for resources, such as nutrients and light. He argued that, if a plant species is able to reduce the availability of a particular resource to a lower level than that required by competing species, it may increase its chances to become the dominant species of its kind or functional group in the community. Two species could coexist if there were two limiting resources, and so on, but there could never be more species than there were limiting resources. In reality, however, many more species can coexist than there are limiting resources, for example due to environmental **heterogeneity**, transient non-equilibrium conditions or more complex food web interactions. Since the 1990s, Tilman and coworkers initiated large-scale experiments on the coexistence of competing species, particularly on the relationship between *ecosystem functioning* and *species diversity* (e.g. Kinzig *et al.* 2001; see also Chapter 2). This type of knowledge helps understanding the problematic relation between ecosystem productivity and plant species richness, also relevant in the context of ecological restoration.

Effects of parasitism

Pathogens and parasites may have a huge impact on **ecosystem structure** and **succession**. In recent times, fungal blights decimated the American chestnut (*Castanea dentata*) from the eastern deciduous forests of the United States, mountain hemlock (*Tsuga mertensiana*) from the Cascadia region of North America, various elms (*Ulmus* spp.) from much of western Europe and a whole range of *Eucalyptus* species from the forests of western Australia (Dobson & Crawley 1994). In each of these cases, the removal of a dominant, late-succession species, as a result of a fungal infestation, led to the development of forests dominated by less competitive species from earlier successional stages. Even more spectacular is the classic example in southern England of the indirect effect on vegetation change due to the viral infection of rabbits (*Oryctolagus cuniculus*), also referred to by Dobson and Crawley (1994). Myxomatosis, caused by the *Myxoma* virus, was accidentally introduced into France in 1952, from where it reached Britain in 1953. In Silwood Park, the result was a 99% reduction in the rabbit population within a few years, which resulted in the transformation of a formerly open, grassy parkland to an oak woodland dominated by pedunculate or common oak (*Quercus robur*). This change has to date proved to be irreversible, even after the recovery of the rabbit population in the 1970s. Apparently, a **threshold of irreversibility** had been crossed (see Chapter 2).

Effects of habitat modification

While the study of *competition* for shared resources and its effects on community structure has a relatively long history, the interest in the effects of habitat modification in terms of *facilitation* of other species has only recently gained momentum (e.g. Bruno *et al.* 2003;

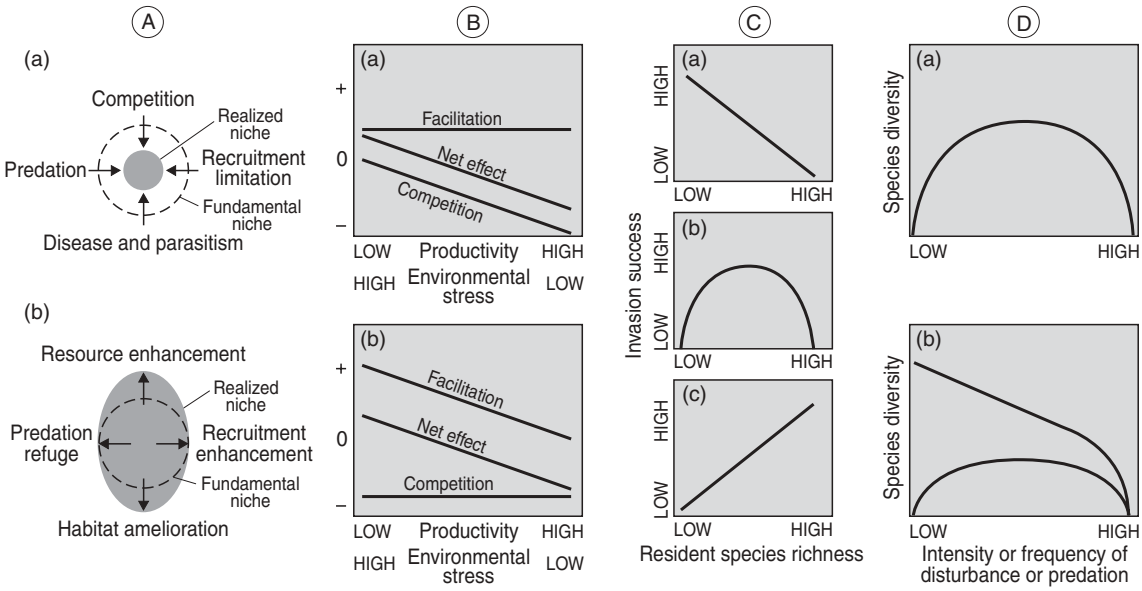

Figure 6.4 Four fundamental models of ecology, with and without facilitation, illustrating paradigm shifts if facilitation is included. (A) The realized niche can be larger than the fundamental niche due to facilitation; (Aa) without facilitation, (Ab) with facilitation. (B) Facilitation may affect the competitive abilities of species along an environmental gradient; (Ba) facilitation weak, constant, (Bb) facilitation strong, variable. (C) Facilitation may have an impact on the success of invaders; (Ca) without facilitation, (Cb or Cc) with facilitation. (D) Facilitation may change the relationship between species richness and ecosystem productivity; and (Da) without facilitation, (Db) with facilitation (lower line, primary space holders; upper line, secondary space holders). (From Bruno *et al.* 2003. Reproduced by permission of Elsevier.)

Brooker *et al.* 2008). Figure 6.4 depicts how fundamentally an ecological theory or model can change when facilitation is included along with competition. Here we focus on changes in the relative importance of competition and facilitation in plant communities as proposed in the so-called *stress-gradient hypothesis* (see Maestre *et al.* 2009). The notion of 'stress' in the latter paper is derived from the work of Grime (1979), who defined stressful environments as those in which producers are limited in their ability to convert energy to biomass. While in Grime's approach only the relative importance of competition changed along a productivity gradient, Maestre and coworkers elaborated on this idea, now also proposing a gradient in facilitation. Central to the stress-gradient hypothesis is the idea that facilitation should be especially common in communities under high physical stress or with high consumer pressure, whereas competition should be the dominant structuring force wherever the physical environment is relatively benign and consumer pressure is less severe. Indeed, overall, the relative frequency of facilitation and competition varies inversely across gradients of physical stress, also known as gradients of ecosystem productivity, whether in space or in time, but there are interesting exceptions (see also Chapter 11). Facilitation may, for instance, affect the competitive abilities of species along an environmental gradient in such a way as to keep it at a low level all along a gradient (Bruno *et al.* 2003), and – adding to the complexity – different facilitative mechanisms may function in a nested hierarchical manner (e.g. Verdú & Valiente-Banuet 2008). For example, experiments with intertidal smooth cordgrass (*Spartina alterniflora*) communities have shown that there exists an hierarchical organization of facilitation among species. The cordgrass provides shade and reduces wave action in these harsh environments, which results in a *cascade* of facilitative effects on other plant and animal species (e.g. ribbed mussels, barnacles, snails and seaweeds) (Altieri *et al.* 2007).

There are also examples of mutually negative interactions between **ecosystem engineers**, for example in the salt marsh–tidal flat interface, where common cordgrass (*Spartina anglica*) and the lugworm (*Arenicola marina*) were found to affect each other negatively by changing their shared biophysical environment in opposite ways (van Wesenbeeck *et al.* 2007). While seedlings of *S. anglica* stabilize the sediment with their roots, preventing *A. marina* from feeding, *A. marina* strongly bioturbates the sediment, preventing *S. anglica* seedlings from establishing. All these examples show the importance of gaining knowledge about basic mechanisms in order to understand long-term cascading effects in communities. Otherwise any attempts at restoration-inspired **intervention** are likely to produce unexpected and possibly undesired results.

Allelopathic species (chemical engineers), excreting organic compounds that can reduce the germination, establishment, growth, survival and/or fecundity of other species, can also have a long-term impact on plant communities, inhibiting succession. In boreal forests, for example, the ground-layer vegetation in late post-fire successions is frequently dominated by dense clones of the dwarf shrub species *Empetrum hermaphroditum*, one of the most widespread plants in the European arctic and boreal biomes. This plant produces large quantities of phenolics and is conspicuously avoided by herbivores. Indeed, it is thought to be responsible for the strong negative effects on tree-seedling establishment and growth of Scots pine (*Pinus sylvestris*), among other plant species, and on microbial activity and plant-litter decomposition rates, thereby contributing to humus accumulation and reduced nitrogen availability (Nilsson *et al.* 1998). In general, phenolics are highly allelopathic under acidic, nutrient-poor soil conditions. In calcareous soils, by contrast, most phenolic compounds are rapidly metabolized by microbial activity and adsorption is high. There are indications that invasive **alien species** may inhibit the germination of native species by chemical interference (Ens *et al.* 2009; see also Chapter 20).

Effects of mutualism

The presence of mycorrhizae has been shown to change the outcome of plant competition in many cases, both for plants associated with arbuscular mycorrhiza and those associated with ectomycorrhiza; they are thus a determinant of plant community structure (e.g. Kiers *et al.* 2000; Stein *et al.* 2009, and references therein). Some mycorrhizal species with a compact structure increase resistance of plants against drought, pathogens, heavy metals and polyphenolic substances (Ozinga *et al.* 1997). In spite of a huge amount of knowledge about the importance of plant–mycorrhiza interactions, including in ecological restoration interventions, actual applications are still largely unexplored (Harris 2009).

Effective restoration of pollinators providing pollinator services in ecological restoration projects has also received too little attention and experimentation, even though much basic information is available (Dixon 2009). **Habitat fragmentation** and other effects of land use – such as agriculture, grazing, herbicide and pesticide use – and the introduction of non-native species have a significant impact on plant–parasite and plant–pollinator interactions (Kwak *et al.* 1998, Taki & Kevan 2007; see also Chapter 7).

6.3.3 Implications for restoration ecology

In our review thus far, we have touched upon a number of potential applications of fundamental ecological insights to ecological restoration projects, but we readily acknowledge that taking all the potential interactions, and all their indirect effects, into account is certainly impossible. Our message is twofold. First, restoration ecologists should realize that **ecosystem functioning** is complex and not easy to initiate, mimic and/or manage. They must, wherever possible, try to integrate the knowledge presented in their efforts to make ecological restoration a success, rather than ignoring the complexity and making a choice for simple solutions. Secondly, and related to this, we welcome and applaud initiatives to scientifically cope with complexity. Searching for general rules and laws, rather than presenting a huge amount of detailed information, continues to be a challenge for scientists. Though this 'coping with complexity' may seem to lead us still farther away from applicability, we consider it useful to inform the reader about promising initiatives.

6.4 COMPLEXITY IN BIOTIC COMMUNITIES

The dynamics of communities is obviously not only determined by interactions between pairs of species: recall the food webs and pollination networks we

mentioned earlier. Indeed, nearly all organisms are embedded in networks of interactions with other organisms consisting of literally thousands of species in many cases; see Olff *et al.* (2009) for an overview of such 'ecological interaction webs'. Dealing with such complexity requires much more than merely doing inventories, or summing up detailed reductionistic sources of information, however useful that may be. Over and above such 'alpha-level' information, restoration ecologists need to be concerned with so-called emerging properties of the biotic community in the ecosystem they are concerned with.

One of the first attempts to understand the implications of ecological interactions within a network of species was launched in the late 1950s by the discussion on why the world is 'green'. Hairston, Smith and Slobodkin argued, after weighing against alternative mechanisms, that the world is green because herbivore density is generally controlled by predators (the so-called *HSS hypothesis*; Hairston *et al.* 1960). Reduction of herbivore numbers by predation would release plants from herbivore control and allow them to reach a high density, explaining why the (terrestrial) world generally has a green appearance. In spite of being fiercely criticized and discussed (Murdoch 1966), the notion that predators can indirectly affect the density of organisms that are the food of the prey they eat (e.g. two trophic levels lower in the community) has stimulated much research, and led to the development of the concept of a 'trophic cascade' (Paine 1980), which implies that consumption not only affects the prey but also affects still lower trophic levels. Trophic cascades have subsequently been suggested for various aquatic ecosystems (e.g. Carpenter *et al.* 1985; Power 1992), and terrestrial ecosystem (e.g. Jefferies 1999; Beschta & Ripple 2009). A recent book by Terborgh and Ested (2010) examines trophic cascades in many of the world's major biomes, including several that are discussed in Part 3 of this volume. Another interesting view upon the HSS hypothesis has been brought forward by Bond and Keeley (2005), who consider fires as a sort of 'selective herbivory'. Indeed, as these authors state, fire has been burning ecosystems for hundreds of millions of years, shaping global biome distributions and significantly altering plant biomass. The effects of fire on, for example, plant competition in consumer-controlled ecosystems are consistent with the predictions of the HSS hypothesis.

Contrary to what was assumed by scientists previously, the theorist Robert May pointed out in 1973 (May 1973) that more complex food webs are less stable (e.g. in terms of their ability to return to equilibrium after disturbance) than simple ones. His models of food webs moreover suggest that the *interaction strength* (in terms of its per capita effect on the prey or the predator) is of crucial importance to food web stability, and that weak interactions can, in principle, compensate for increased food web complexity. May's pivotal work strongly stimulated research into food webs in a wide range of ecosystems, and led to important insights into the processes and properties that stabilize ecological communities (Pimm 1984). First, food webs were found to be strongly compartmentalized, for example interactions within food webs are grouped in smaller subcommunities, where interactions between species within a compartment are stronger than between species of different compartments (Krause *et al.* 2003). This reduces the linking intensity within food webs, and makes the food web more stable and robust. Other studies revealed that the relative strength of interactions within food webs follows a pattern: weak bottom-up effects occur at lower trophic levels, while weak top-down effects predominate at higher trophic levels (de Ruiter *et al.* 1995; Neutel *et al.* 2007). Modelling exercises of the latter authors showed that the latter pattern strongly improves the stability of food webs, when compared to models where strong and weak interactions are randomly distributed across the web.

Up to the late twentieth century, ecological theory focused on the distribution of feeding relations within communities. Obviously, species can interact in a number of alternative ways, as described in the previous section. How does this affect our understanding of the network structure and dynamics of ecological communities? Studies on mutualistic networks between plants and animal pollinators and seed dispersers revealed that these networks have a different structure than consumptive networks (e.g. food webs); they are highly nested, where more generalist plants and animals interact with each other to form a dense core of interactions, to which the more specialist species are attached (Bascompte *et al.* 2003). In other words, mutualistic networks form a nested structure rather than a compartmented structure that is typical of food webs (Figure 6.5). How does this affect community dynamics? Nestedness was found to reduce interspecific competition and enhance the number of coexisting species. Hence, the structure promotes species persistence and structural stability, similar to the importance of compartmentation and interaction

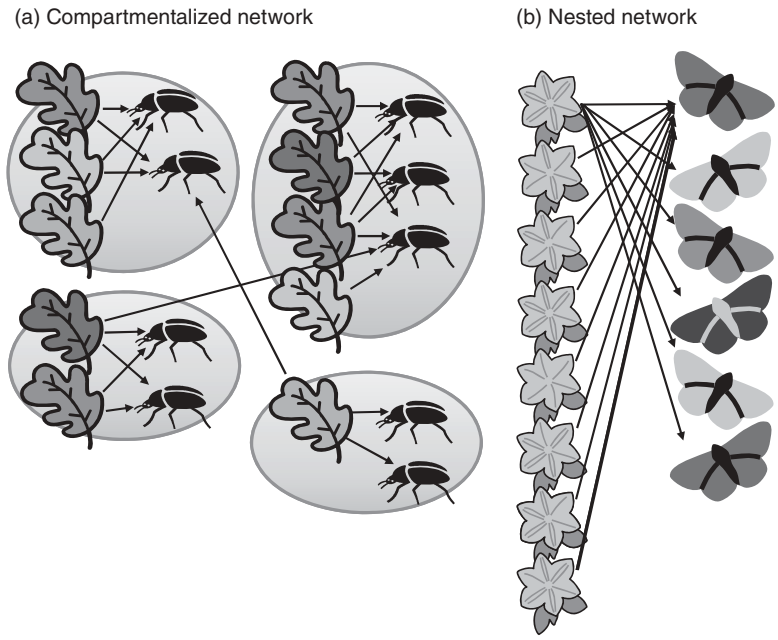

Figure 6.5 Network architecture. (a) Species form networks of interdependence such as illustrated in this figure. The nature of the interaction may be antagonistic (when one species benefits but the other loses, for instance by predation of one by the other) or mutualistic (when both species benefit from the interaction). (b) Consumptive interactions tend to be arranged in compartments, whereas mutualistic interactions tend to be nested. (Modified from Bascompte 2010.)

strength patterns in food webs. Most natural communities, however, consist of a range of possible interactions being mutualistic interactions, consumptive interactions, interference, and interactions mediated via the environment. To integrate these possible interactions into a unified understanding of the network structure remains one of the scientific challenges for the coming years.

6.5 RESTORATION OF ECOSYSTEMS: A FEW RECOMMENDATIONS

In this chapter, we have presented some of the basic concepts of the ecology of ecosystems and biotic communities, which may help those engaged in the ecological restoration and rehabilitation of degraded and impaired ecosystems based on a scientific approach to the problem. We have also alerted the reader to a number of potential implications of developing theories. So far, however, we have not referred to the criteria for the successful restoration of degraded, damaged or destroyed ecosystems that were formulated in the Primer for Ecological Restoration of SER (2004) in terms of nine attributes of restored ecosystems (see Chapter 2). What kind of recommendations can we derive from our discussion of the structure and functioning of ecosystems and biotic communities with reference to these attributes?

We recommend that ecologists and their collaborators who aim to re-establish 'a characteristic assemblages of the species that occur in the reference ecosystem' they have chosen or constructed, to explicitly consider the importance of both negative and positive interactions between and among species within the network of the community, and the very real possibility of trophic cascades, both of which can differ in restored ecosystems as compared to their respective reference systems. Note that we have hardly dealt with the effects of alien invasive species as compared to the effects of indigenous species; for this topic, please see Chapter 20.

The condition that 'all functional groups necessary for the continued development and/or stability of the

ecosystem are represented' requires attention for the problematic relationship between ecosystem functioning and species richness (see Chapter 2). Ecosystem functions include productivity, nutrient cycling, decomposition and so on. In restoration projects that make use of functional groups, it is often assumed, or hoped, that the effects of increasing species richness on ecosystem productivity probably works through changes in functional diversity. However, there is still an unsolved dilemma that requires attention. Some experimental results favour the *redundant-species hypothesis* (i.e. only a few keystone species contribute to the productivity of the ecosystem), while others support the *rivet hypothesis*, whereby almost all or a minimum number of species essentially contribute to ecosystem productivity (for further reading, see e.g. Loreau *et al*. 2002).

We agree with the criterion that the restored ecosystem should be 'suitably integrated into a larger ecological matrix existing within the landscape, with which it interacts through abiotic and biotic flows and exchanges'. On this subject, readers should also refer back to Chapter 4, where the 'Landscape Functional Analysis' approach was introduced for monitoring and evaluating ecological restoration projects, and also study Chapter 5, which presented the basic components of modern landscape ecology. Later, readers will also find much food for thought in Chapters 16–19 on wetlands, which explicitly illustrate how ecosystems are open systems embedded within larger landscapes.

One of the most important criteria for ecosystem restoration as formulated by the *SER Primer* (SER 2004) is that restored ecosystems should be 'resilient'. The reader will recall from Chapter 2 that the notion of **resilience** is an emergent characteristic or attribute of an ecosystem expressing its ability to return to an earlier steady state after major disturbance. In principle, the more resilient an ecosystem (or restored ecosystem) is, the faster it returns to the previous steady state. Here we distinguish more explicitly between these two aspects of resilience, as they have been named and defined differently by various authors of differing backgrounds, reviewed by, for example, Gunderson (2000) and Groffman *et al*. (2006). Not recognizing the difference in the practice of ecological restoration may cause confusion. Resilience in ecological systems ('ecological resilience') is defined as the ability to return to the previous equilibrium, or as the magnitude of degradation that can be absorbed before the ecosystem redefines its structure and develops towards a new equilibrium. Once a system surpasses a threshold of irreversibility, it is disturbed and may shift to an alternative steady state, as in the above-mentioned case of shallow lakes. Resilience in engineering systems ('engineering resilience') is defined as the return time to a previous state of relative equilibrium. Only in the latter case can different 'degrees of ecosystem resilience' be distinguished.

This brings us to a final take-home message. In this chapter, we have tried to introduce the foundations of ecosystem ecology, and point out that **ecosystems** are considered the central focus of **ecological restoration**. While navigating at the interface between theory and practice, many readers may sometimes find that these two poles are incompatible. Indeed, in the restoration ecology literature there is much debate on the subject; see for example Cabin (2011).

For several reasons, we have chosen in this chapter not to confine ourselves to those parts of ecological theories about, and insights into, the structure and functioning of ecosystems that have already been proven to be applicable to ecological restoration. We are convinced that gaps between theory and practice can only be overcome once they have been explicitly recognized, for example the recognition of problems related to the applicability of theories of 'resilience' and 'complexity'. We take the view that basic, curiosity-driven science and applied science do go together, and both are needed – from all the relevant disciplines and professions – in order to tackle the highly complex problems faced in most situations where ecological restoration is necessary. In fact, this is the critical insight of **transdisciplinarity** and **sustainability science** (Chapters 2 and 22). We welcome and applaud initiatives in search of further exploring the important interface between restoration ecology and the ecological restoration of ecosystems.

ACKNOWLEDGEMENT

We are grateful to James Aronson for his indispensable and much appreciated editorial contributions to this chapter.